



FIRST PERMIAN RECORD OF *BRANCHIOSAURUS* (AMPHIBAMIFORMES) FROM THE BOSKOVICE BASIN (CZECH REPUBLIC)

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Abstract: Augusta (1947) described *Moraverpeton remesi* and *Branchiosaurus* sp. from the Zbýšov Horizon of the Padochov Formation (earliest Asselian, early Permian) at Zbýšov in the Boskovice Basin (Moravia, Czech Republic), and assigned them to the family Branchiosauridae. This original amphibian material is very probably lost. New branchiosaurid material from the Zbýšov Horizon of Zbýšov and Moravský Krumlov are hereby described and is consistent with the described amphibian material from Augusta (1947). ‘*Moraverpeton*’ *remesi* AUGUSTA, 1947 is clearly a branchiosaurid and is assigned to the genus *Branchiosaurus* FRITSCH, 1876 as *B. remesi*. A neotype is established for *B. remesi*. This species is defined by a unique character combination of 11 features, e.g., the wide, near squarish supratemporal, the early dermal ornament with pits and ridges on median skull elements, and the maxilla with about 20 teeth.

The aquatic fauna of the Zbýšov lake mainly consists in juvenile bivalves, with rarer occurrences of conchostracans, small actinopterygian fishes, *Acanthodes*, freshwater chondrichthyans and algae. This lake was at times amphibian dominated. The *Branchiosaurus remesi* population from the Zbýšov lake belongs to the stream type, suggesting high oxygen levels, possibly due to inflow from a river. The aquatic fauna of the Moravský Krumlov lake was fish-dominated by actinopterygians and xenacanthids, with only one single branchiosaurid specimen which very probably belongs to *B. remesi*.

Key words: Amphibamiformes, genus *Branchiosaurus*, early Permian, Boskovice Basin, systematics, palaeoecology

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Introduction

The Boskovice Basin is famous for the abundance and diversity of discosauriscid stem-amniotes recovered from its early Permian strata (e.g., Augusta 1936a, b, Špinar 1952, Klembara 1997 ff.). Branchiosaurids, however, were for a long time only known from one occurrence in this basin (Augusta 1947). In 2005, further very interesting branchiosaurids were discovered during a joint excavation of the Museum of Eastern Bohemia in Hradec Králové and the Technical University Bergakademie Freiberg near Kočov and have since been published (Werneburg et al. 2023). They were found only a few centimeters above a layer package with many discosauriscids. Meanwhile, we know about eight occurrences of branchiosaurids from different stratigraphic

levels in the Boskovice Basin, which are currently being studied (Mikudíková, Štamberg, Werneburg).

Augusta (1947) described, alongside plants and bivalves, the small amphibians *Moraverpeton remesi* and *Branchiosaurus* sp. from a locality near Zbýšov in Moravia. Unfortunately, the original material described by Augusta (1947) must now be considered as lost. Several attempts to localise it were made a few decades ago (RW) and most recently in 2024 (SŠ). Enquiries were addressed to curators of the palaeontological collections at the Natural History Museum in Brno, National Museum Prague, and Charles University in Prague, but no trace of the specimens was found.

Fortunately, new amphibian material from the type locality was collected by the former Ph.D. student at the Charles University Prague (CUP-NC), Jan Němec (together with SŠ,

1970). In 1991, two of the authors (RW and JWS) also found some skeletons from the same locality (NHMS-WP). In addition, a unique small skeleton was found in the Zbýšov Horizon at Moravský Krumlov (SŠ, 2007), which presented similarities to ‘*Moraverpeton*’ *remesi*. We assume that the historical and new amphibian material of the Zbýšov horizon corresponds to the finds of Augusta (see Materials and Methods). All new specimens are the base for the following description and revision of ‘*Moraverpeton*’ *remesi* and *Branchiosaurus* sp. (Augusta 1947).

Institutional abbreviations

CUP-NC	Charles University Prague, Němec-collection, Czech Republic
MHK	Museum of Eastern Bohemia Hradec Králové, Czech Republic
NHMS-WP	NaturHistorisches Museum Schloss Bertholdsburg Schleusingen, Germany

Geological setting

The Boskovice Basin currently occupies an area of about 500 km². This half graben, nearly 100 km long and 3 to 10 km wide, runs in +/- NNE-SSW direction. It is located in the eastern part of the Bohemian Massif, between the Lugodanubicum and Moravosilesicum (Opluštil et al. 2017, 2022). The Boskovice Basin is divided by the transverse Tišnov-Kouřim Elevation (Havlena 1964, Jaroš and Malý 2001) into two parts: the southern Rosice-Oslavany Sub-basin containing late Carboniferous and early Permian sediments, and the Letovice Sub-basin containing only early Permian (Asselian to Artinskian) sediments (Opluštil et al. 2017). The total thickness of the sedimentary successions in both sub-basins is considerable and, according to Jaroš (1962), reaches about 5,000 to 6,000 m, although according to geophysical measurements the sediment thickness is of about 2,000 m (Malý 1993) or 3,000 m (Dopita et al. 1985). The sedimentary fill of the basin is subdivided on the basis of lithology and cyclicity from bottom to top into the Rosice-Oslavany, Padochov, Veverská Bítýška and Letovice formations (Jaroš and Malý 2001). Of these formations, the Veverská Bítýška and Letovice Formations are present only in the northern part of the Letovice Sub-basin (Jaroš and Malý 2001, Pešek 2004).

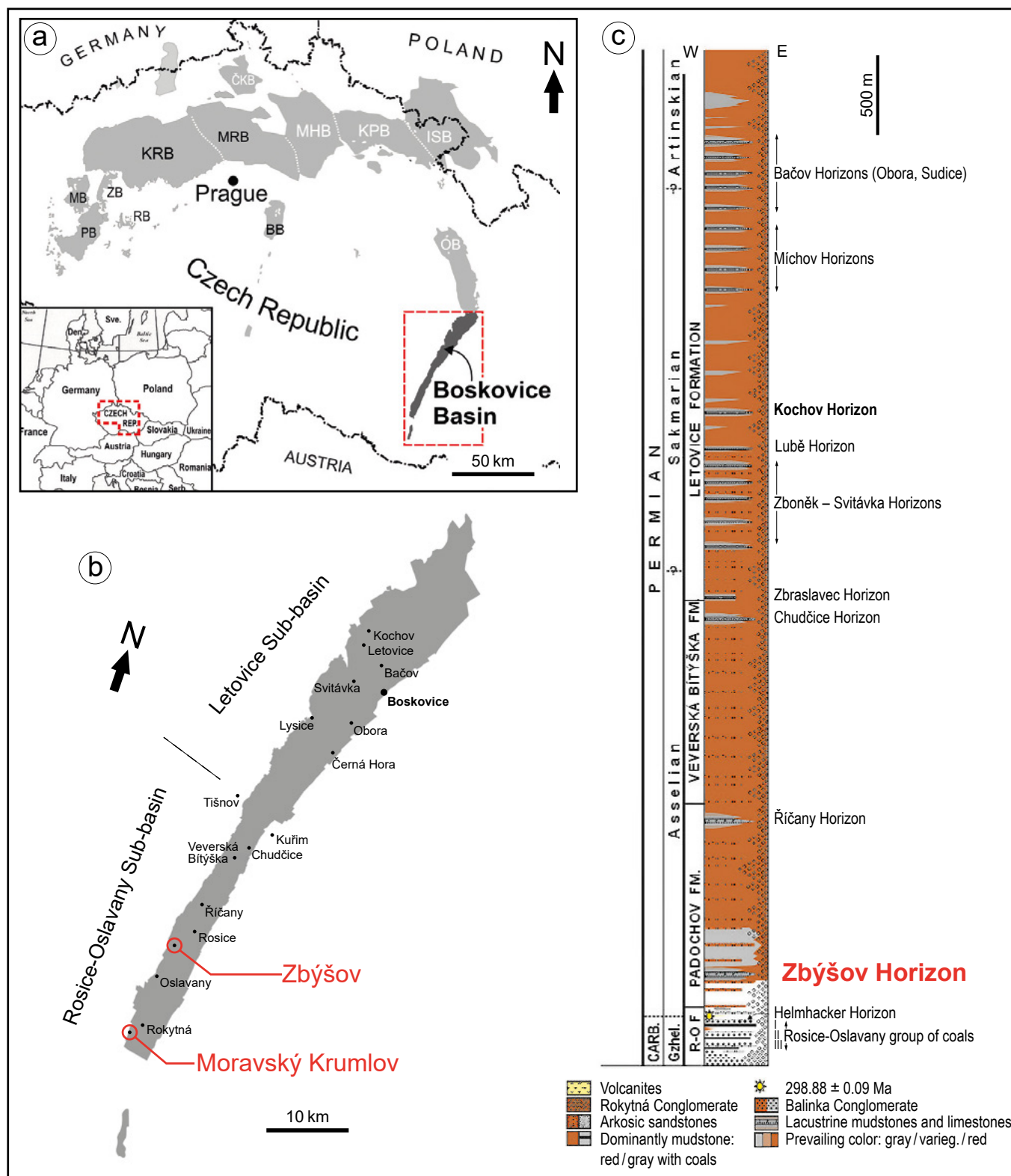
The oldest Rosice-Oslavany Formation mostly consists of late Carboniferous sediments. Recent CA-ID-TIMS U-Pb zircon dating of acid volcanic rocks deposited just below its upper boundary has provided an age of 298.88 ± 0.09 Ma, corresponding almost exactly to the Gzhelian–Asselian boundary (Opluštil et al. 2017). The overlying Padochov Formation is of Asselian age. In the northern Letovice Sub-basin, the younger Veverská Bítýška Formation and Letovice Formation are also of Permian age. Their sedimentation is regarded as Asselian in age (Opluštil et al. 2017, Štamberg 2014), although flora (Šimůnek and Martínek 2009) and fauna (Schneider and Werneburg 2012, Werneburg et al. 2023) occurrences suggest that the deposition of the Letovice Formation continued up into the early Artinskian.

The branchiosaurids described in this study have been recovered from the Zbýšov Horizon of the Padochov Formation (Text-fig. 1). The Padochov Formation, up to 1,200 m-thick, conformably overlies the Rosice-Oslavany Formation and consists mainly of sandstones and mudstones. Its lower part, about 50 m-thick, is predominantly formed by grey conglomerates, sandstones, mudstones and claystones. Right above, follows a 60 m-thick succession of increasingly red coarse clastics with intercalated gray mudstones, which contain a 3 to 4 m-thick horizon of gray silt- to claystones and bituminous carbonates: the Zbýšov Horizon. The overlying 1,000 m of the Padochov Formation is characterised by a monotonous alternation of red sandstones and mudstone with another gray carbonate, referred as the Říčany Horizon, situated 900 m above the Zbýšov Horizon (Jaroš and Malý 2001, Opluštil et al. 2013). The early Asselian age of the Zbýšov Horizon of the Padochov Formation is well constrained by radioisotopic and biostratigraphic data: the top of the underlying Rosice-Oslavany Formation is dated to 298.88 ± 0.09 Ma while the Říčany Horizon (close to the top of the Padochov Formation) is dated to the early Asselian by the recovery of a blattoid insect wing assigned to the *Sysciophlebia balteata*–*Spiloblattina homigtalensis* zone (Schneider and Werneburg 2012, Schneider et al. 2020).

The fauna described here comes from two localities of the Zbýšov Horizon. The type locality of ‘*Moraverpeton*’ *remesi* AUGUSTA, 1947 is “*Za pilou dolu Antonín*” (“Behind the sawmill of the Antonín mine”). The locality and its fossil content were first described by Augusta (1947), who reported, in addition to amphibians, scales and body fragments of actinopterygian fishes, spines of *Acanthodes gracilis*, four species of bivalves, unspecified insect remains, and a rich flora (Augusta 1947). Kukalová (1955, 1959) and Schneider (1983, 1984) described several insects from this locality as Protorthoptera, Palaeodictyoptera, and Dictyoptera.

The second site, containing a single amphibian occurrence, is Moravský Krumlov “*Za lesním úřadem*” (“Behind the forest office”). The first mentions of this locality date from the end of the 19th century, with the findings of a rich Permian flora. Subsequently, several bivalve species, rare isolated scales of actinopterygian fishes (Mrázek 1948, Augusta and Čepěk 1948) and the blattoid insect *Phyloblatta moravica* STEHLÍK, 1932 were described from this locality. A detailed history of the Moravský Krumlov “*Za lesním úřadem*” site’s research is given by Ivanov (2003).

New research on the site began in 2005, when, with the help of a group of students from the Technical University Bergakademie Freiberg, additional occurrences of gray-black bituminous carbonates were discovered at several places on the slope above the Rokytňá River, within the locality Moravský Krumlov “*Za lesním úřadem*”. Excavations continued in the following years carried out by the staff of the Museum of Eastern Bohemia of Hradec Králové. The sedimentary succession of the “*Za lesním úřadem*” locality comprises the Rokytňá conglomerate, which gradually becomes finer towards the top and passes into coarse-grained sandstones. The sandstones are overlaid by the fossiliferous Zbýšov Horizon. At its base, the horizon consists of a 35 cm-thick gray to gray-brown siltstone with abundant flora,



Text-fig. 1. Geographic and geologic setting of the branchiosaur localities Zbýšov and Moravský Krumlov in the Boskovice Basin, Czech Republic (CR). a: Position of Carboniferous and Permian continental basins in the CR. Abbreviations: PB – Pilsen, MB – Manětín, RB – Radnice, ŽB – Žihle, KRB – Kladno-Rakovník, MRB – Mšeno-Roudnice, ČKB – Česká Kamenice, MHB – Mnichovo Hradiště, KPB – Krkonoše-Piedmont, ISB – Intra-Sudetic, BB – Blanice, OB – Orlice. Boskovice Basin is marked with a red frame (modified after Opluštil et al. 2017). b: Outcrops Zbýšov “Za pilou dolu Antonín” (Behind the sawmill of the Antonín mine) and Moravský Krumlov “Za lesním úřadem” (Behind the forest office) in the southern part of the Boskovice Basin are indicated by red stars. c: litho- and chronostratigraphy of the Boskovice Basin with the fossiliferous marker horizons; Zbýšov Horizon is marked by red colour (modified after Opluštil et al. 2017, based on Jaroš 1962, Pešek 2004, and Schneider et al. 2020).

including relatively large branches (up to 30 cm-long) of the conifer *Walchia* and fragments of *Pecopteris* fern-leaves. It transits upwards into a succession of >1m-thick black bituminous shales and mm-scale bedded carbonate-clay laminites with intercalated 30 cm-thick black limestone to pelitic carbonate containing rare plant and some animal remains. Besides the skeleton of a branchiosaurid amphibian, the now updated fauna of the “Za lesním úřadem” locality includes numerous remains of the actinopterygian fish *Neslovicella*, teeth and spines of the freshwater shark *Bohemiacanthus*, rare *Acanthodes* spines and up to 5 cm-long coprolites (Štamberg 2013). It should be noted that the rich “Autunian” flora described from Moravský Krumlov (Šimůnek and Martínek 2009, Opluštil et al. 2013) originates from gray-brown to gray-green siltstones situated at least 10 m above the faunal layer.

Materials and methods

Unfortunately, the original amphibian material of the Zbýšov Horizon described by Augusta (1947) seems to be lost (see Introduction). It is only figured as small photos without visible anatomical details on pl. II: figs 1 (anterior skeleton) and 3 (skeleton of 3 cm length) for *Branchiosaurus* sp., and figs 2a (complete skeleton) and 2b (posterior skeleton) for ‘*Moraverpeton*’ *remesi*. All these skeletons present a characteristic branchiosaurid morphotype, with very small skull length between 5 and 7 mm and short ribs with widened ends. Augusta (1947) assigned all these skeletal remains to the family Branchiosauridae (p. 188) noting differences with *Discosauriscus*, extensively recovered from the Boskovice Basin (Augusta 1936a, b). Nevertheless, Schoch and Milner (2014: 116) assigned ‘*Moraverpeton*’ *remesi* to a “discosauriscid batrachosaur” without anatomical reference. Maybe this placement based on the description of an “interclavicle with a long and strike processus at the back” in Augusta (1947: 222). This posterior process is not recognizable in the photos (Augusta 1947: pl. II, fig. 2a, b) and is highly questionable. The other features described by Augusta (1947: 221–223) do not correspond to the anatomy of *Discosauriscus*, but clearly fit that of branchiosaurids: (1) “20–22 trunk vertebrae” in contrast to 23 to 24 presacral vertebrae in *Discosauriscus* (Klembara and Bartík 1999), (2) “several rows of minute spines of gill teeth” which are not known in discosauriscids (Klembara 1997), (3) “phyllospondylic vertebrae” only with paired neural arches (which were considered characteristic of branchiosaurids at the time), (4) “parasphenoid with processus cultriformis” (the cultriform process is most likely meant as rod-shaped which is common in the temnospondyls and in contrast to the more triangular one in *Discosauriscus* (Klembara 1997) – all these features are not known from seymouriamorphs.

Augusta (1947) described “*Branchiosaurus* sp.” based on two specimens in bad and incomplete preservation (Augusta 1947: 223, pl. II, figs 1, 3). Given the poor preservation state of the material, the lack of informative photography’s and of diagnostic features, the assignment of these two specimens to *Branchiosaurus* sp. is not supported and considered hereby as dubious.

The new branchiosaurid material of Zbýšov is stored in the Němec-Collection at Charles University Prague (CUP-NC 51, 61, 77, 84, 87, 95, 98, 165). It comprises about 15 specimens, which were studied intensively using silicone casts (stored in the NHMS under the original numbers) and subsequently illustrated. Three additional branchiosaurid skeletons (stored in the NHMS: NHMS-WP 751, 752 and 6225) were recovered during an excursion in 1991 (RW and JWS) and have also been illustrated (NHMS). A unique small branchiosaurid was found in the Zbýšov horizon from Moravský Krumlov in 2007 (SŠ; MHK 72779/1).

The skeletons of the NHMS were prepared mechanically by Georg Sommer (NHMS) using pneumatic needles. Photographs were taken with a Nikon D5100 camera. Drawings were prepared with a “camera lucida” at a Zeiss research binocular. Comparisons with other branchiosaurid material is mainly based on personal observation of original specimens.

Systematic palaeontology

Order Temnospondyli ZITTEL, 1888
Superfamily Dissorophoidea BOLT, 1969
Clade Amphibamiformes SCHOCH, 2018
Family Branchiosauridae FRITSCH, 1879

Genus *Branchiosaurus* FRITSCH, 1876

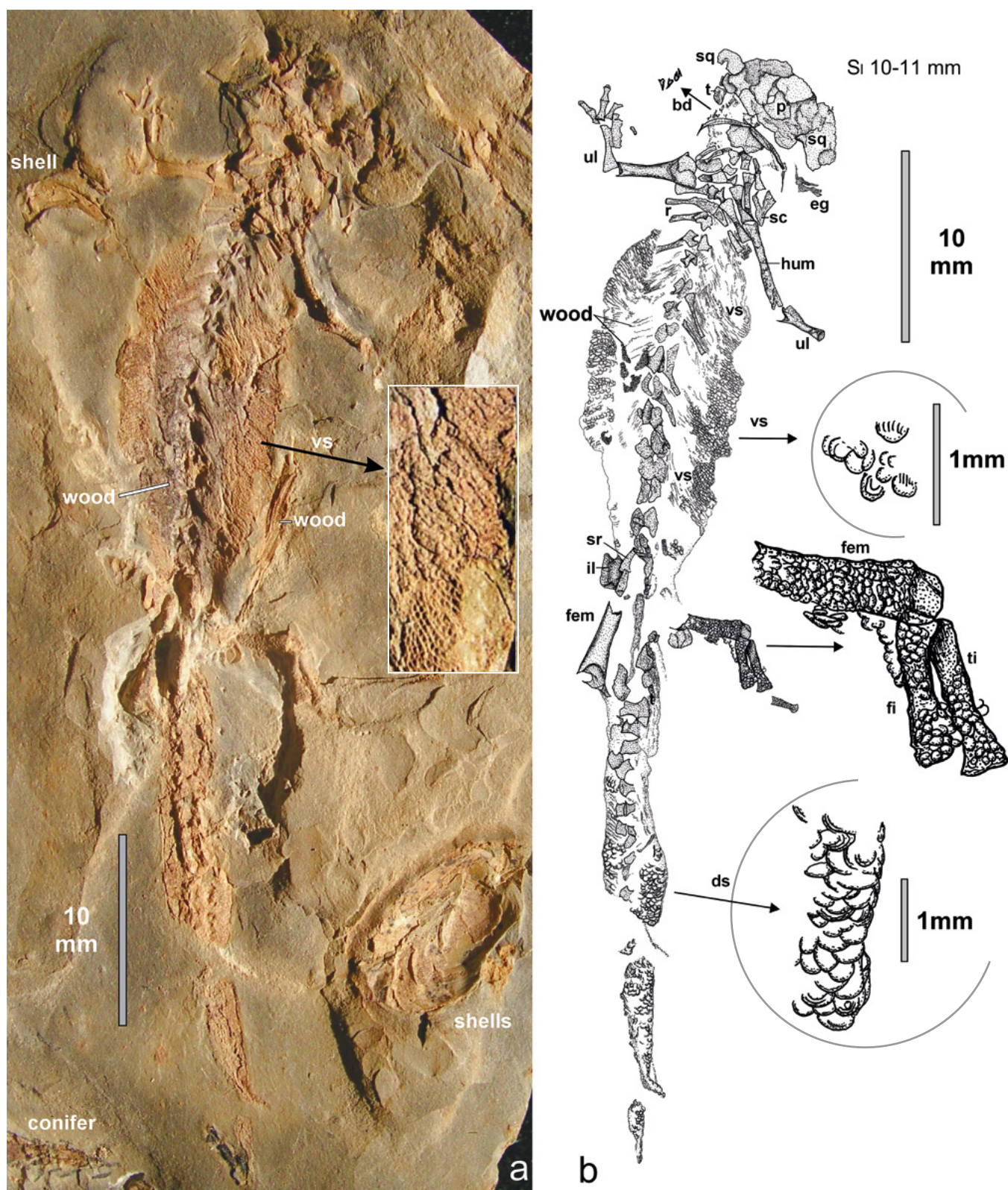
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|-------------|---|
| Partly 1906 | <i>Protriton Fayoli</i> ; Thevenin, pl. X, figs 6, 8. |
| Partly 1910 | <i>Protriton Fayoli</i> ; Thevenin, pl. I, figs 8, 10. |
| 1947 | <i>Moraverpeton remesi</i> ; Augusta, pl. II, fig. 2a, b. |
| 1947 | <i>Branchiosaurus</i> sp.; Augusta, pl. II, figs 1, 3. |
| 2007 | <i>Moraverpeton remesi</i> , discosauriscid; Milner, Klembara and Dostál, p. 711. |
| 2014 | <i>Moraverpeton</i> , ?discosauriscid batrachosaur; Schoch and Milner, p. 116. |

Type species. *B. salamandroides* FRITSCH, 1876, here fig. 11a.

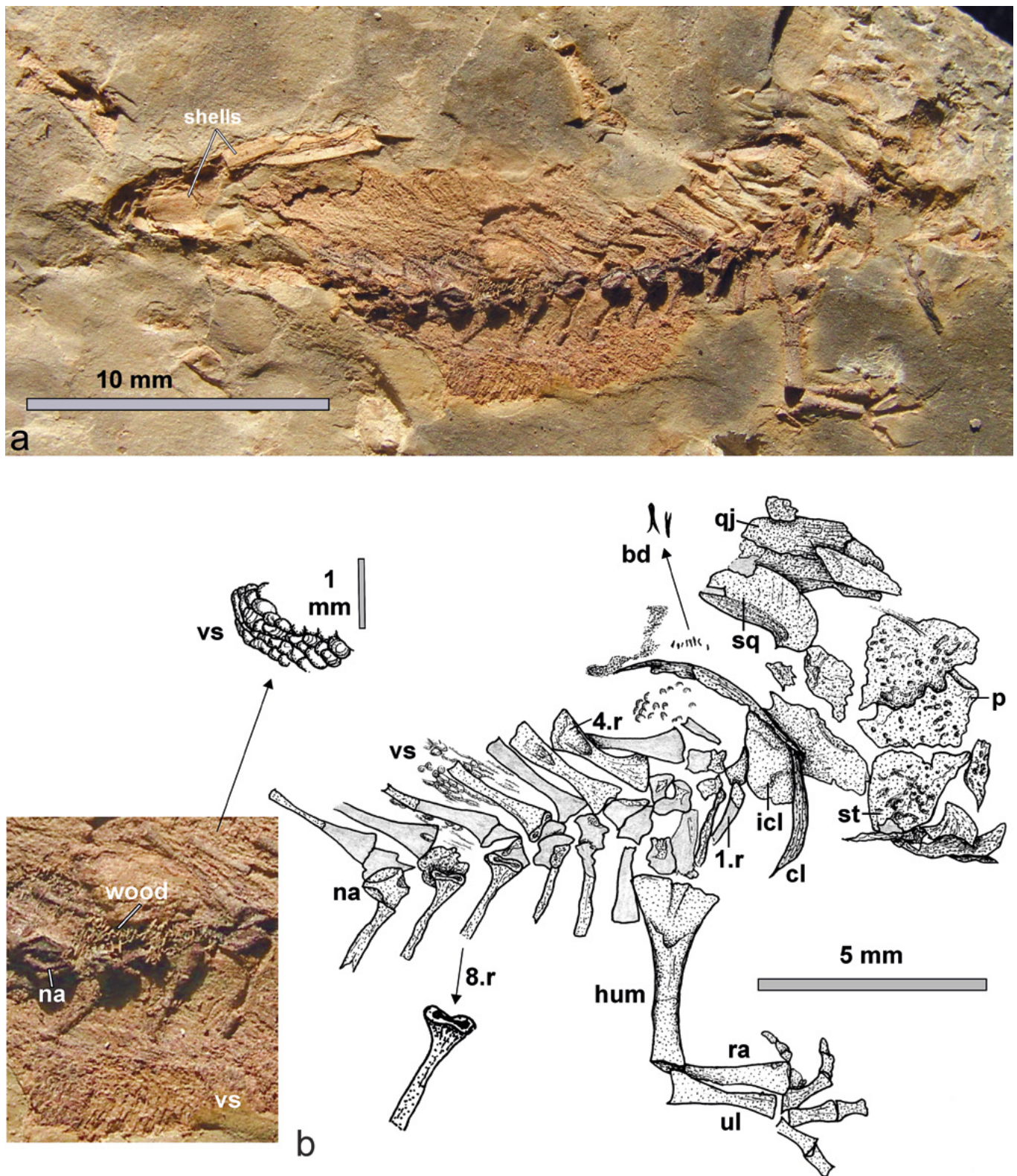
Other species. *B. commentryensis* WERNEBURG, 2019, here Text-fig. 11b, c; *B. remesi* (Augusta 1947) (see below).

Diagnosis. Branchiosaurids with the following unique character combination:

- (1) Prefrontal-postfrontal in contact.
 - (2) Anteriorly extended jugal even at an early stage.
 - (3) Posterior skull table foreshortened ($H_I/S_I = 0.27\text{--}0.42$).
 - (4) Relatively wide interorbital region ($IO_w/S_I = 0.25\text{--}0.38$).
 - (5) Maxilla elongated.
 - (6) Relatively short and broad palatine, small ectopterygoid and robust palatinal ramus of pterygoid.
 - (7) Branchial denticles with elongated single needle or paired needles, mostly attached to a rounded base.
 - (8) Ventral osteoderms well ossified and thickened in a V-shape.
 - (9) Relatively elongated interclavicle ($Icl_I/S_I = 0.13\text{--}0.38$).
 - (10) 20–22 presacrals.
- (modified from Boy 1987, Werneburg 1987, Schoch and Milner 2008, and Werneburg 2019).



Text-fig. 2. *Branchiosaurus remesi* (AUGUSTA, 1947) from Zbýšov – the largest well-preserved specimen in ventral view. a, b: Photo and drawing of the skeleton, NHMS-WP752a. Abbreviations: bd – branchial denticles, ds – dorsal/lateral scales, eg – external gills, fem – femur, fi – fibula, hum – humerus, icl – interclavicle, il – ilium, na – neural arches, p – parietal, r – ribs, sc – scapulocoracoid, sq – squamosal, sr – sacral rib, st – supratemporal, t – tabular, ti – tibia, ul – ulna, vs – ventral scales.



Text-fig. 3. *Branchiosaurus remesi* from Zbýšov. a, b: Photos and drawing from the counterpart NHMS-WP752b. Abbreviations: bd – branchial denticles, cl – clavicle, hum – humerus, icl – interclavicle, na – neural arches, p – parietal, qj – quadratojugal, r – ribs, ra – radius, sq – squamosal, st – supratemporal, ul – ulna, vs – ventral scales.

***Branchiosaurus remesi* (AUGUSTA, 1947)**

Text-figs 2–10, 11d, e, 12a, b, h–l

- 1947 *Moraverpeton remesi*; Augusta, pl. II, fig. 2a, b.
 1947 *Branchiosaurus* sp.; Augusta, pl. II, figs 1, 3.
 2014 *Moraverpeton*, ? discosauriscid batrachosaur;
 Schoch and Milner, p. 116.
 2022 Discosauriscidae indet.; Calábková et al., fig. 2.

Neotype. NHMS-WP751a, b; an anterior skeleton (Text-fig. 5) corresponding to a larval individual, and a well-preserved skull (length 8.9 mm) in dorsal and ventral views, and well preserved anterior postcranial elements. Its skull bones are the basis for the tentative reconstruction of the largest recorded dorsal skull roof (Text-fig. 10b).

Type horizon. Gray mudstone of the Zbýšov Horizon, lower part of Padochov Formation (earliest Asselian, early Permian).

Type locality. “Za pilou dolu Antonín” – dump behind the Saw-Mill of the Antonin-Mine near the village of Zbýšov, Boskovice Basin, Moravia, Czech Republic.

Diagnosis. A new species of *Branchiosaurus* with the following unique character combination:

- (1) Narrow preorbital skull with elongated nasal and vomer, and long-oval orbit (max. orbital length-to-width ratio: 1.48–1.57) (shared with *Branchiosaurus salamandroides* and many other branchiosaurids, except for *B. commentryensis*).
- (2) Elongated squamosal (shared with *B. salamandroides* and many other branchiosaurids, except for *B. commentryensis*).
- (3) Wide, near squarish supratemporal, which is 1.2 times

wider than long (shared with *B. salamandroides*, *Melanerpeton eisfeldi*, *Xerodromeus gracilis*, *Piasmotriton kochovi*, except for *B. commentryensis*).

(4) Early dermal ornament with pits and ridges on median skull elements (shared with *Piasmotriton kochovi*).

(5) Maxilla with about 20 teeth (shared with other branchiosaurids, except for *B. salamandroides* with 35–36 teeth, not known in *B. commentryensis*).

(6) Premaxilla with about 12 teeth (shared with other branchiosaurids, except for *B. salamandroides* with 14–15 teeth, not known in *B. commentryensis*).

(7) Posteromedial sclerotical elements elongated and narrow (shared with *Melanerpeton*, *Xerodromeus gracilis*).

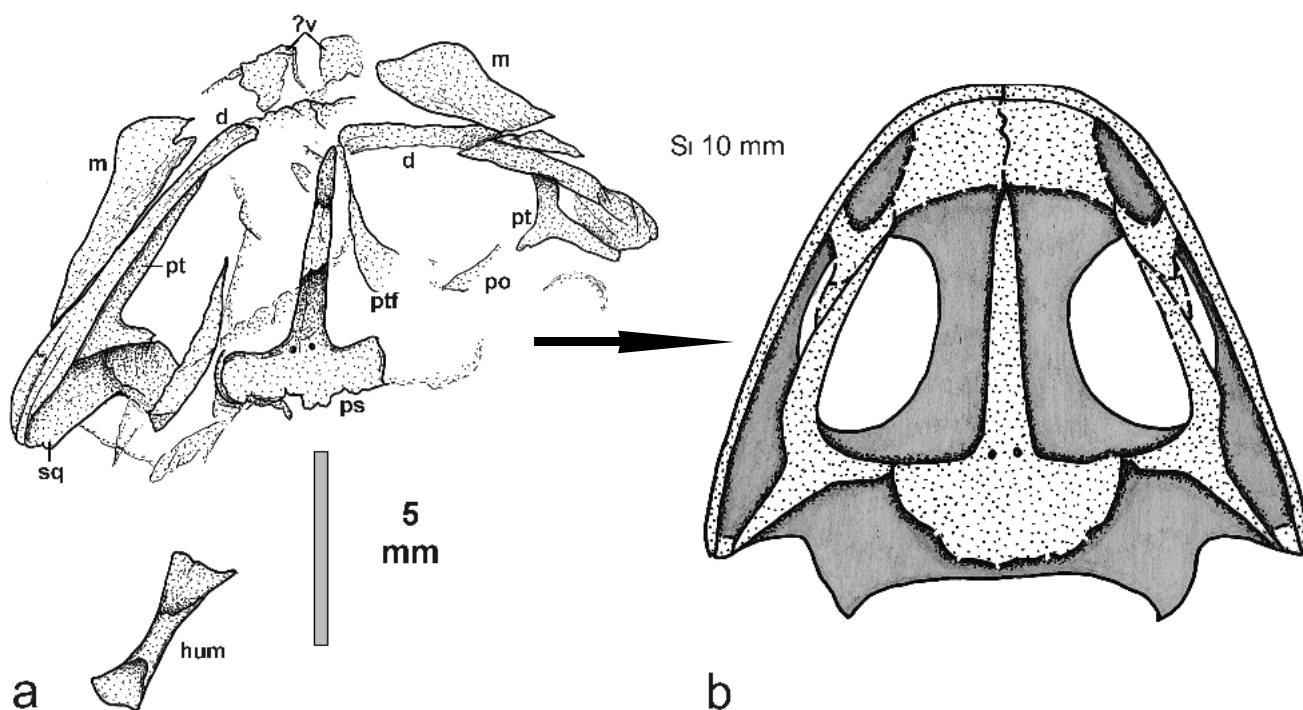
(8) Basal plate of parasphenoid only with carotid foramina and without foramina for nervus palatinus VII (shared with all branchiosaurids, except for *B. salamandroides*, *B. commentryensis*).

(9) Hyobranchial skeleton of *flagrifer*-type (shared only with *Apateon flagrifer*, *A. caducus*).

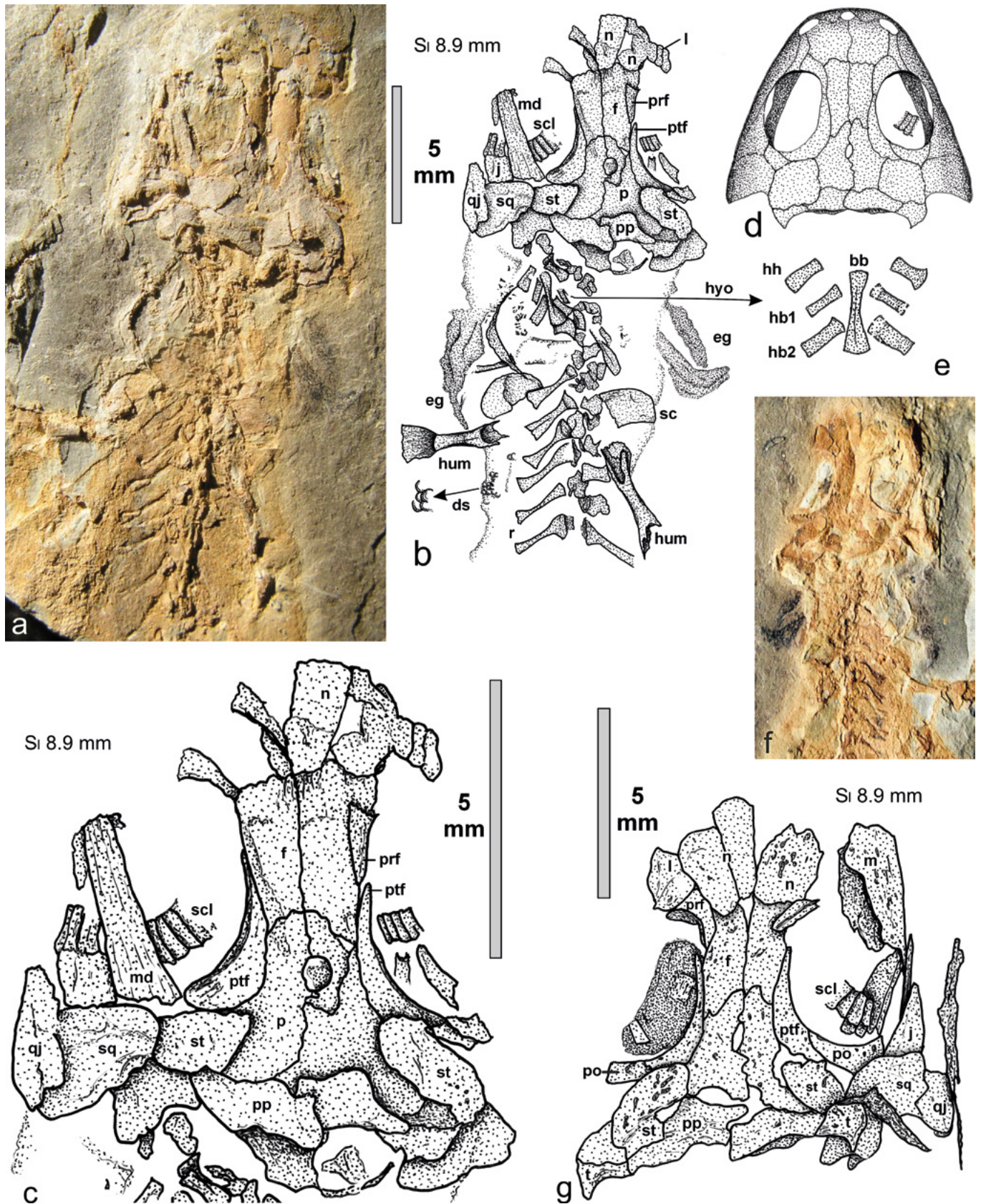
(10) Thoracic ribs with double joint head (shared with *Apateon pedestris*).

(11) Ischium elongated and relatively narrow (shared with *B. salamandroides* and many branchiosaurids, except for *B. commentryensis*).

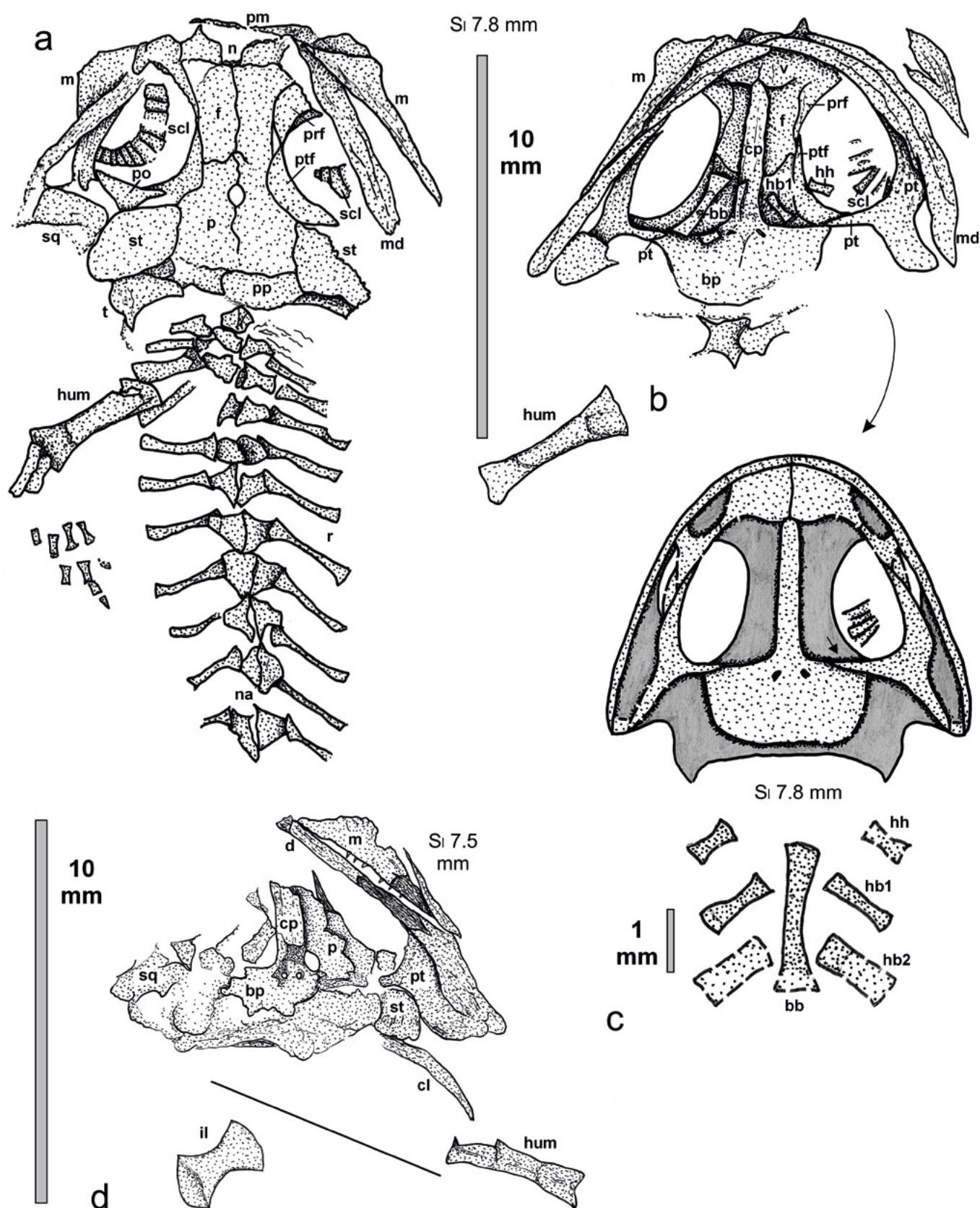
Other material. From the type locality Zbýšov: CUP-NC84 (Text-fig. 4), CUP-NC61 (Text-fig. 6a–c), CUP-NC98 (Text-figs 6d, 7a, 8a), CUP-NC51 (Text-fig. 8c), CUP-NC165 (Text-fig. 8e), CUP-NC95 (Text-fig. 8d), CUP-NC87 (Text-fig. 8f), and CUP-NC77 (Text-fig. 7d); NHMS-WP752 (Text-figs 2, 3), NHMS-WP6225 (Text-figs 7b, c, 8b). From the type horizon of Moravský Krumlov (“Za pilou dolu Antonín” – behind the forest office, Boskovice Basin): MHK72779/1 (Text-fig. 9).



Text-fig. 4. *Branchiosaurus remesi* from Zbýšov, large skull in ventral view (a, CUP-NC84) and tentative reconstruction of the palate (b, see Text-fig. 10d). Abbreviations: bp – basal plate of parasphenoid, cp – cultriform process, d – dentary, ec – ectopterygoid, hum – humerus, m – maxilla, pl – palatine, po – postorbital, ps – parasphenoid, pt – pterygoid, ptf – postfrontal, sq – squamosal, v – vomer.



Text-fig. 5. *Branchiosaurus remesi* from Zbýšov – the NEOTYPE-specimen in dorsal view (a–c, NHMS-WP751a), with a tentative reconstruction of the dorsal skull roof (d, see Text-fig. 10b) and the reconstruction of the hyobranchial apparatus (e), the NEOTYPE-specimen in ventral view (f, g, NHMS-WP751b). Abbreviations: bb – basibranchiale, ds – dorsal/lateral scales, eg – external gills, f – frontal, hb1, 2 – hypobranchial 1 or 2, hh – hyohyal, hum – humerus, hyo – hyobranchial apparatus, j – jugal, l – lacrimal, m – maxilla, md – mandibula, n – nasal, p – parietal, po – postorbital, pp – postparietal, prf – prefrontal, pt – pterygoid, ptf – postfrontal, qj – quadratojugal, r – ribs, sc – scapulocoracoid, scl – sclerotical ring elements, sq – squamosal, st – supratemporal, t – tabular.



Text-fig. 6. *Branchiosaurus remesi* from Zbýšov – anterior skeleton in dorsal (a, CUP-NC61a) and ventral view (b, CUP-NC61b) with reconstruction of the palate (b, see Text-fig. 10c) and hyobranchial apparatus (c, CUP-NC61b); ventral skull and few postcranial bones (d, CUP-NC98b). Abbreviations: bb – basibranchiale, bp – basal plate, cl – clavicle, cp – cultriform process, d – dentary, f – frontal, hb1, 2 – hypobranchial 1 or 2, hh – hyohyal, hum – humerus, il – ilium, m – maxilla, md – mandibula, n – nasal, na – neural arches, p – parietal, po – postorbital, pp – postparietal, prf – prefrontal, pt – pterygoid, ptf – postfrontal, r – ribs, scl – sclerotical ring elements, sq – squamosal, st – supratemporal, t – tabular.

Table 1. Biometric characters of the branchiosaurid *Branchiosaurus remesi* in comparison with other species of *Branchiosaurus*. Measurement abbreviations: H_1 – postorbital midline length of skull from level of posterior margins of orbits, H_w – postorbital width of skull between lateral margins of supratemporals, huml – maximum length of humerus, icl – maximum length of interclavicle, IO_w – minimum interorbital width, ot-or – minimum length between anterior otic notch and posterior orbit, ra_1 – maximum length of radius, S_1 – midline skull length. The blue ratios are the smallest and the red ratios are the largest ratios vertically.

Specimens (Inv.-No.)	Figs	S_1 in mm	IO_w/S_1	H_w/S_1	H_1/S_1	ot-or/ S_1	hum/ S_1	ra_1/hum_1	icl/ S_1
NHMS-WP 752	2	10–11	–	–	–	–	0.46	0.56	0.13
CUP-NC 84	4a	10	–	–	–	–	0.48	–	–
NHMS-WP 751	5	8.9	0.26	0.79	0.29	0.22	0.51	–	–
CUP-NC 61	6a–c	7.8	0.26	0.93	0.33	–	0.43	0.43	–
CUP-NC 98b	6d, 7a	7.5	0.29	0.82	0.27	0.16	0.35	0.59	–
NHMS-WP 6225	7b–c	6	0.27	0.82	0.31	0.20	0.54	0.50	0.26
CUP-NC 95	8d	5	0.31	–	0.29	–	–	–	–
CUP-NC 87a	8f	4.3	0.27	0.94	0.34	–	–	–	–
Summary	<i>B. remesi</i>	4.3–11	0.26–0.31	0.79–0.94	0.27–0.34	0.16–0.22	0.43–0.54	0.43–0.59	0.13–0.26
Comparison	<i>B. commentryensis</i>	5.4–8.2	0.32–0.38	0.75–0.89	0.30–0.42	0.16–0.20	0.40–0.51	0.44–0.66	0.20
Comparison	<i>B. salamandroides</i>	5–12.7	0.25–0.31	0.79–1.13	0.28–0.40	0.25	0.36–0.56	0.43–0.57	0.29–0.38

Comparative description. All important and well-preserved bones are described, figured and compared with related taxa if necessary.

General morphology. The about fifteen specimens are relatively small-sized with skull lengths between 4 mm and 11 mm. Specimens with a skull length of up to 6 mm and a largely ossified skull roof (Text-fig. 8f) still fall into stage C of Schoch and Witzmann (2024), but even with a skull length of 6 mm (Text-fig. 7c, d) starts here stage D with well ossified limbs and girdles.

Shared characters such as the well ossified scalation, the massive and short ilium, the squarish supratemporal, the elongated posteromedial sclerotic elements and early established dermal sculpturing indicate that they all belong to the same taxon.

The dermal sculpture of the dorsal skull roof is pronounced starting in the ontogenetic stage with a skull length of only 5–6 mm (Text-fig. 8b, d). The median skull bones are most intensively sculptured with many pits and few short ridges.

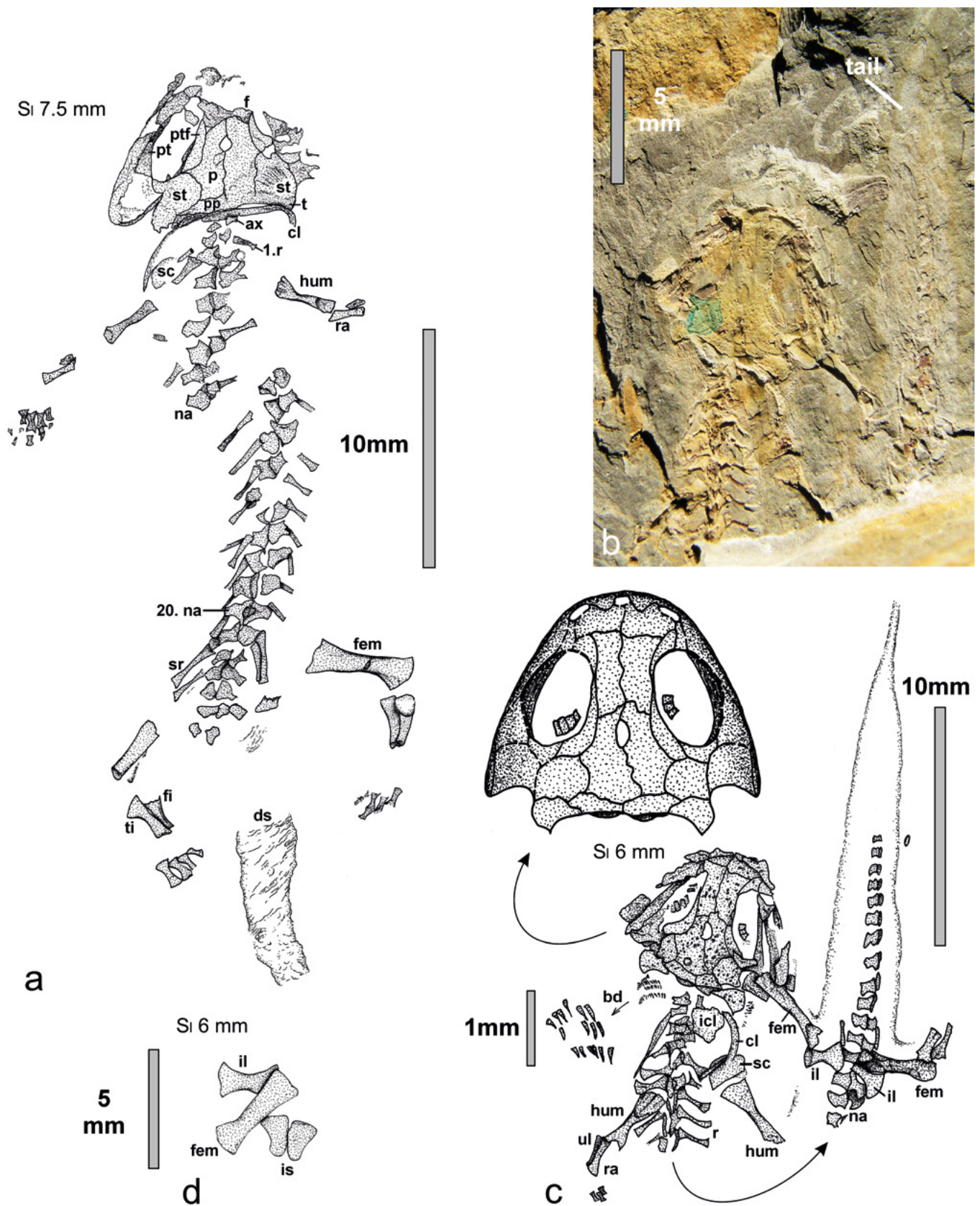
The degree of ossification of the dermal scales and vertebral column especially is relatively high (Text-figs 2d, 3a) in comparison with equal-sized branchiosaurids. The intensive dermal sculpture, the high degree of ossification and the bilobed joint heads of the ribs in this ontogenetic stage indicate a species with a fast ontogenetic development.

Skull roof. The preorbital region of the skull is elongated due to the lengthened nasal and vomer. The orbit is long-oval shaped – about 1.5 times longer than wide (max. orbital length-to-width ratio: 1.48–1.57). That's in contrast to *Branchiosaurus commentryensis* (Werneburg 2019) where the nearly circular orbit is only 1.16 times longer than wide (Text-fig. 11b, d). The general shape of the skull is relatively elongated in the ontogenetic stage below 10 mm skull length (only 1.21–1.24 times wider than long) because of the elongated preorbital skull. This character is shared with *B. salamandroides* but contrasted to *B. commentryensis* (1.32 times wider than long; Text-fig. 11a, b, d). The posterior skull table is foreshortened ($H_1/S_1 =$

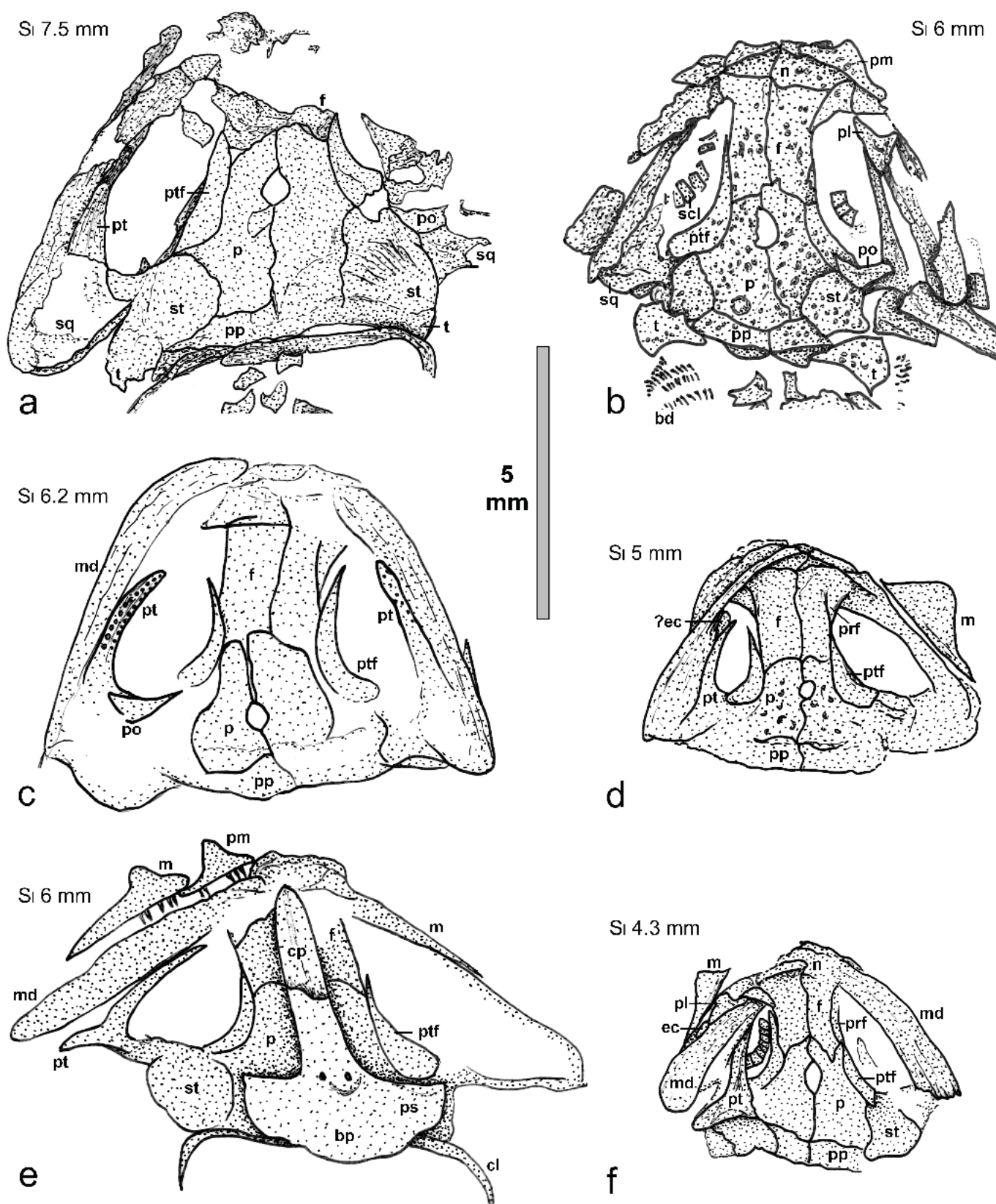
0.27–0.34; Tab. 1). The orbital margin is laterally closed by the connected jugal and maxilla.

The posteromedial directed sclerotic elements are elongated and narrow like in *Melanerpeton* and *Xerodromeus gracilis* (Schoch and Werneburg 2023). The jugal has an anteriorly extended process even at an early stage below 10 mm skull length and its posterior base is relatively narrow too (Text-fig. 5d). The maxilla is elongated and bears about 20 teeth (in contrast to *B. salamandroides* with 35–36 teeth, see Werneburg 2012). The dorsomedial process of the maxilla and premaxilla is already very high in its earliest stage with skull length of 5–6 mm (Text-fig. 8d, e). The premaxilla bears about 12 tooth places. The nasal is elongated and as long as wide (skull length 9 mm). The lacrimal is narrow (Text-fig. 5d) and contacts the orbital margin and the naris. The prefrontal is relatively large with a well-developed posterior process and dorsoventral rim. Pre- and postfrontal are in clear contact. This plesiomorphic character is shared with the other *Branchiosaurus*-species, *Apateon dracyiensis*, *Tungussogyrinus*, *Milnererpeton*, *Anthracobamus*, and *Montceaubatrachus*. The postfrontal has an elongated anterior process and a narrow posterior part. The frontal is relatively wide. The interorbital region is relatively wide ($IO_w/S_1 = 0.26–0.31$), shared with *B. salamandroides* but in contrast to *B. commentryensis* (Tab. 1). Parietal and frontal are of equal length ($S_1 = 9$ mm). The near squarish supratemporal is 1.2 times wider than long (shared with *B. salamandroides*, *Melanerpeton eisfeldi*, *Xerodromeus gracilis*, except for *B. commentryensis*). The tabular and postparietal are of medium length, the tabular bears a posterior process. The postorbital is very short; its width varied. The squamosal is relatively elongated like in *B. salamandroides* but in contrast to *B. commentryensis* (Text-fig. 11). The quadratojugal is elongated and relatively narrow (Text-figs 5e, 8b). The quadrate condyle lies clearly anterior to the occipital condyle.

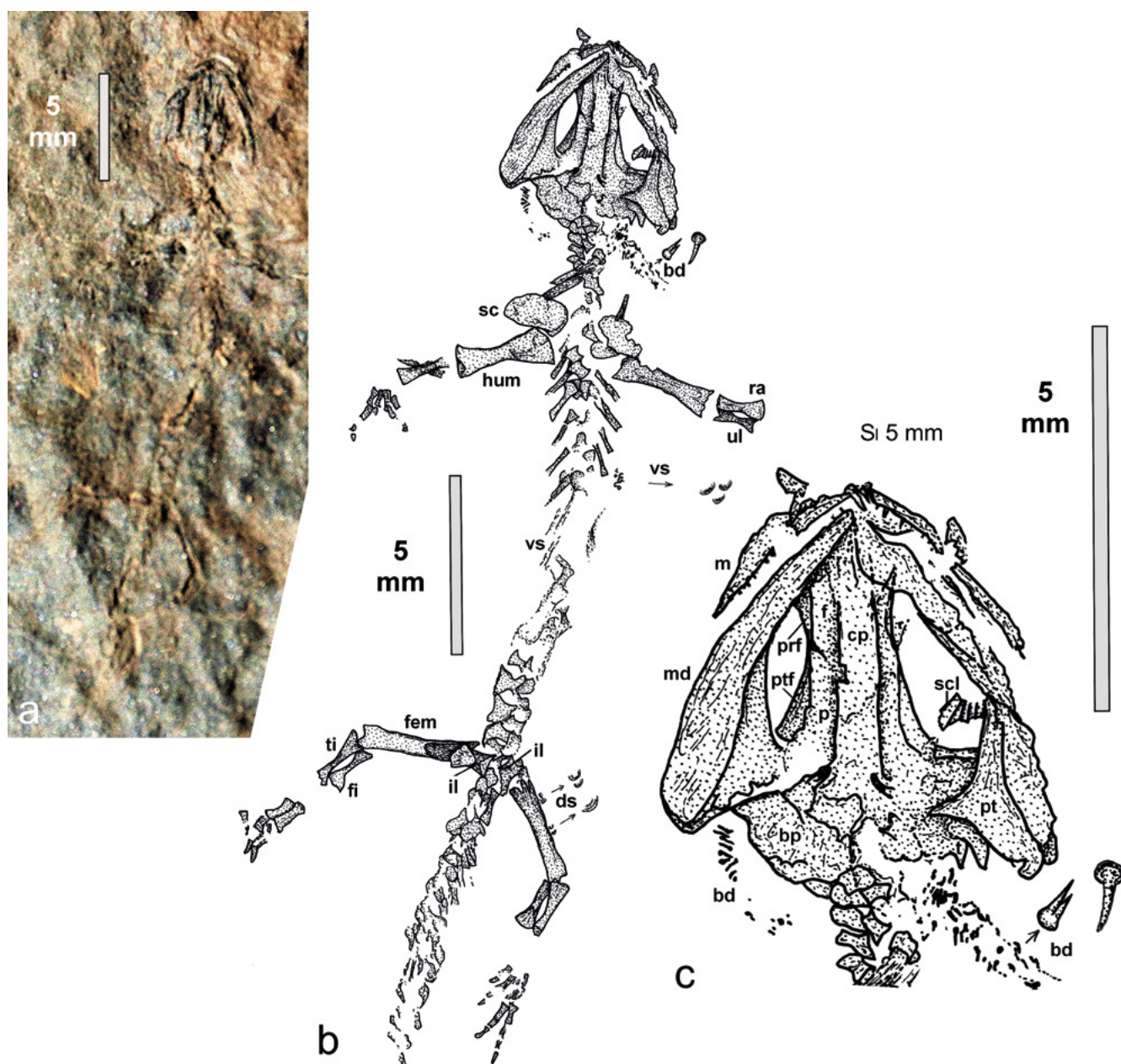
Palate. The vomer is elongated and longer than in *B. commentryensis* (Text-fig. 11).



Text-fig. 7. *Branchiosaurus remesi* from Zbýšov – smaller skeletons. a: In dorsal view (CUP-NC98a). b, c: In ventral view with imprint of the dorsal skull roof and the complete tail (NHMS-WP6225), with reconstruction of the dorsal skull roof (c, see Text-fig. 10a). d: Pelvis and femur (CUP-NC77). Abbreviations: ax – axis, bd – branchial denticles, cl – clavicle, ds – dorsal/lateral scales, f – frontal, fem – femur, fi – fibula, hum – humerus, icl – interclavicle, il – ilium, is – ischium, na – neural arches, p – parietal, pp – postparietal, pt – pterygoid, ptf – postfrontal, r – ribs, ra – radius, sc – scapulocoracoid, sr – sacral rib, st – supratemporal, t – tabular, ti – tibia, ul – ulna.



Text-fig. 8. *Branchiosaurus remesi* from Zbýšov – smaller skulls. a: In dorsal view (CUP-NC98a). b: In ventral view with imprint of the dorsal skull roof (NHMS-WP6225). c: In ventral view (CUP-NC51). d: In dorsal view (CUP-NC95). e: In ventral view (CUP-NC165a). f: In ventral view (CUP-NC87b). Abbreviations: bd – branchial denticles, bp – basal plate, cl – clavicle, cp – cultriform process, ec – ectopterygoid, f – frontal, m – maxilla, md – mandibula, n – nasal, p – parietal, pl – palatine, pm – premaxilla, po – postorbital, pp – postparietal, prf – prefrontal, ps – parasphenoid, pt – pterygoid, ptf – postfrontal, scl – sclerotal ring elements, st – supratemporal, t – tabular.

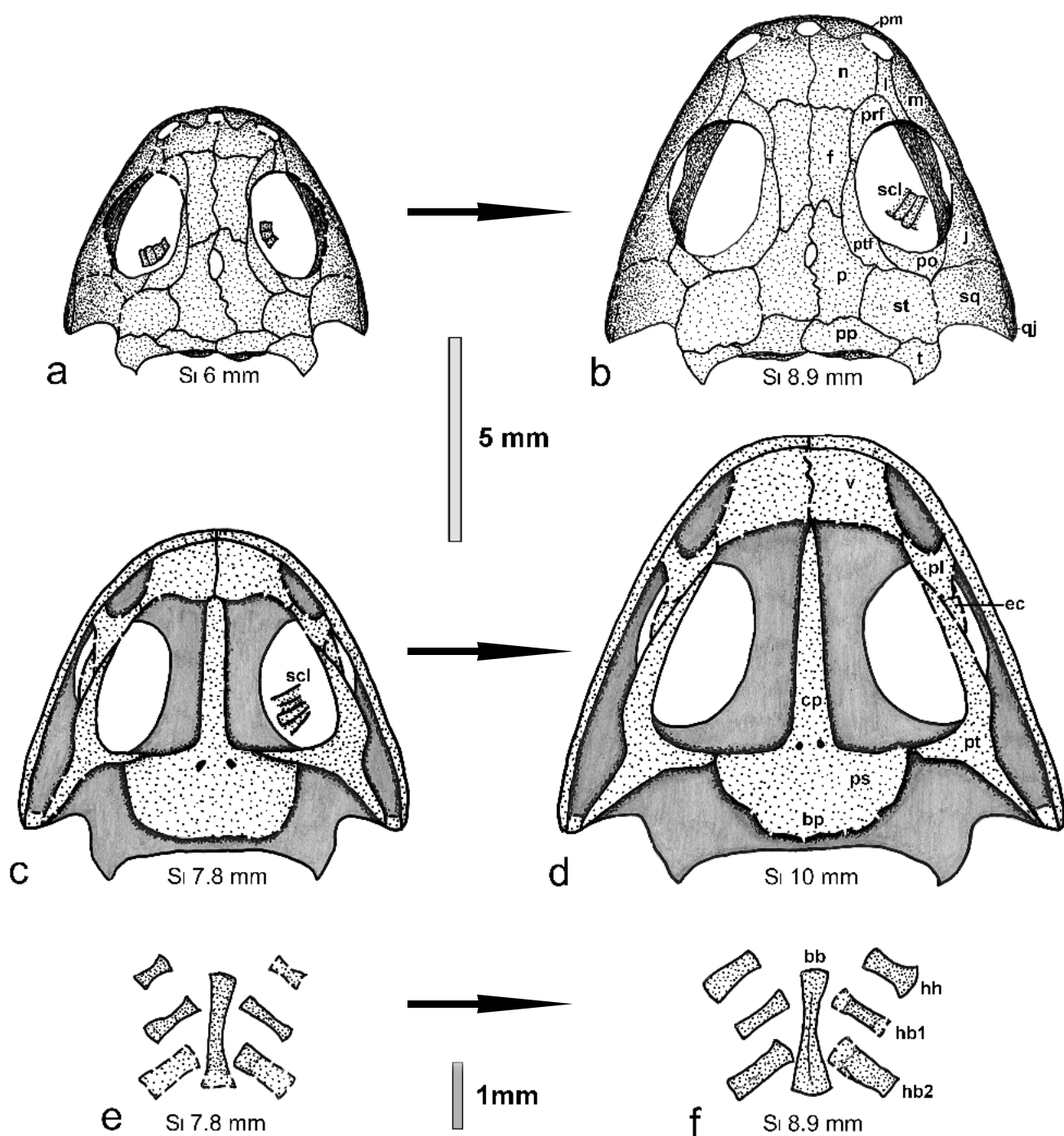


Text-fig. 9. *Branchiosaurus remesi* from the Zbýšov Horizon of Moravský Krumlov – an unique specimen in ventral view (a–c; MHK72779/1). Abbreviations: bd – branchial denticles, cp – cultriform process, f – frontal, fem – femur, fi – fibula, hum – humerus, il – ilium, m – maxilla, md – mandibula, p – parietal, prf – prefrontal, pt – pterygoid, ptf – postfrontal, ra – radius, sc – scapulocoracoid, scl – sclerotical ring elements, t – tabular, ti – tibia, ul – ulna, vs – ventral scales.

The robust palatine is short and wide (Text-fig. 8b, f). The ectopterygoid is very short (Text-fig. 8d, f). The pterygoid is peculiar. Its palatine process and basiptyergoid process are of equal proportions than in other *Branchiosaurus*-species (Text-figs 10d, 11c). An implied transverse process at the palatine process and a medial elongated basiptyergoid process of the pterygoid which lies on anterior basal plate of the parasphenoid – both characters are recorded in only one specimen (left pterygoid, Text-fig. 6b) and fall within the variability range of the pterygoid from *Branchiosaurus remesi* with a skull length of 8 mm (Text-figs 10c, d, 11c, e). The parasphenoid has a relatively wide basal plate that is two times wider than long, but not as wide as in *Piasimotriton kochovi* (2.5 times wider than long). The cultriform process is very narrow. The entire ventral parasphenoid is smooth and bears

no indication of sculpturing or denticles (Text-fig. 10c-d). The basal plate bears no foramina for nervus palatinus VII (shared with all branchiosaurids, but in contrast to *B. salamandroides* and *B. commentryensis*).

Visceral ossifications. The hyobranchial skeleton is of the *flagrifer*-type and is only shared with *Apateon flagrifer* and *A. caducus* (Text-fig. 10e, f; Werneburg 2009: fig. 8). The median element is the elongated and slightly curved basi-branchial. The elongated hypobranchial 1 is equal in length to the hypobranchial 2, but the latter element is wider. The hypohyal is up to a skull length below 8 mm shorter than both hypobranchials and similarly narrow as the hypobranchial 1 (Text-fig. 10e). But with a skull length of 9 mm, the hypohyal is more elongated and of equal length as the hypobranchial 1 and similarly wide as the hypobranchial 2 (Text-fig. 10f). The

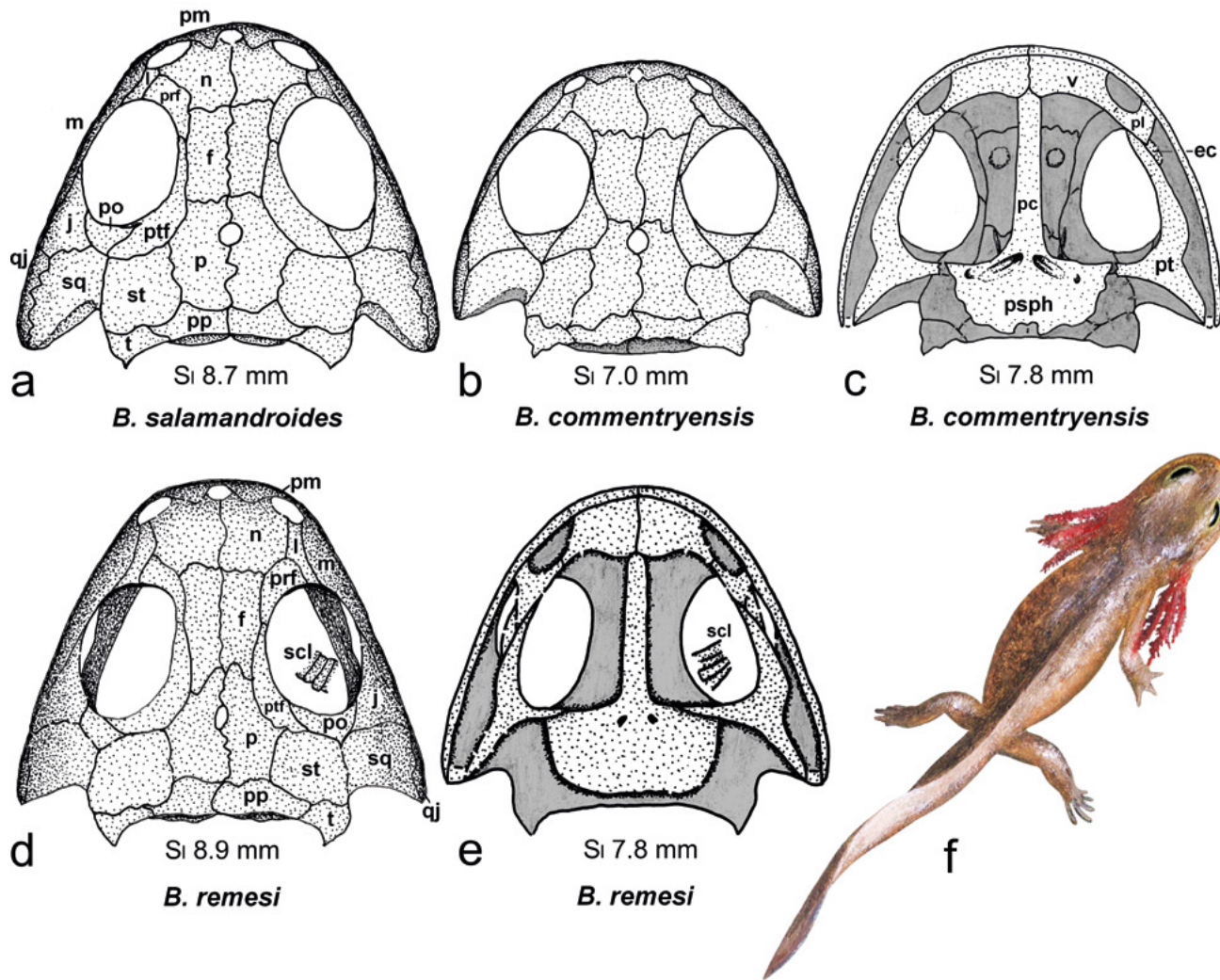


Text-fig. 10. Ontogeny in *Branchiosaurus remesi* with tentative reconstructions of the dorsal skull roof (a, b), the ventral palate (c, d) and the hyobranchial apparatus (e, f). Abbreviations: bb – basibranchial, bp – basal plate, cp – cultriform process, ec – ectopterygoid, f – frontal, hb1, 2 – hypobranchial 1 or 2, hh – hyohyal, j – jugal, l – lacrimal, m – maxilla, n – nasal, p – parietal, pl – palatine, pm – premaxilla, po – postorbital, pp – postparietal, prf – prefrontal, ps – parasphenoid, pt – pterygoid, ptf – postfrontal, qj – quadratojugal, scl – sclerotal ring elements, st – supratemporal, t – tabular, v – vomer.

hyobranchial skeleton differs from that of *B. commentryensis* which is of the *kontheri*-type (Werneburg 2019: fig. 10a). It is not recorded in *B. salamandroides*. Three relatively short external gills are preserved (Text-fig. 5a, c). The branchial denticles are recorded as isolated needles (Text-figs 3b, 7c, 8b, 9) or sometimes together with a distinct rounded base with needles (Text-fig. 9c). The needles may be single or paired (Text-figs 3b, 9). Both cases of preservation are documented in one specimen of *B. commentryensis* (Werneburg 2019: fig. 11e). The stapes is not recorded.

Lower jaw. Without details preserved.

Postcranial skeleton. The paired neural arches are well ossified ($S_1 = 10\text{--}11$ mm; Text-figs 2d, 3b). Vertebral centra are not ossified. The vertebral column has 20–22 presacral vertebrae (Text-figs 2, 7a). The ribs are relatively short, straight and the 4–5th ribs are more widened distally. At least the 7–9th ribs have developed a bilobed joint head ($S_1 = 10\text{--}11$ mm; Text-fig. 3b). The sacral rib is elongated and probably narrow. The humerus is elongated ($\text{huml}/S_1 = 0.43\text{--}0.54$; Tab. 1) as in most branchiosaurids. The radius is elongated, about half



Text-fig. 11. Comparison of dorsal skull roof (a, b, d) and ventral palate (c, e) reconstructions of the genus *Branchiosaurus*, additionally its life reconstruction (f) (artwork by Frederik Spindler, PALAEONAVIX). Abbreviations: bp – basal plate, ec – ectopterygoid, f – frontal, j – jugal, l – lacrimal, m – maxilla, n – nasal, p – parietal, pc – cultriform process, pl – palatine, pm – premaxilla, po – postorbital, pt – pterygoid, pp – postparietal, prf – prefrontal, psph – parasphenoid, pt – pterygoid, ptf – postfrontal, qj – quadratojugal, scl – sclerotal ring elements, st – supratemporal, t – tabular, v – vomer.

the length of the humerus ($ra/hum_1 = 0.43\text{--}0.59$). The ulna is shorter than the radius and more curved. The femur is longer than the humerus and in one specimen ($S_1 = 5$ mm; Text-fig. 9b) the femur is longer than half of the skull length.

The pectoral girdle is partly recorded. The interclavicle is elongated at an early stage, almost as wide as long with a skull length of 6 mm (Text-fig. 12a) which is well comparable with *B. salamandroides* (Text-fig. 12d). The specimen with a skull length of 10–11 mm has a wider interclavicle, even if originally it was probably a little longer (Text-fig. 12b). The clavicle has a long-oval, narrow ventral blade. The cleithrum is only recorded as a small rod (Text-fig. 3b). The scapulocoracoid is characteristically half-moonlike at early skull lengths (Text-figs 5c, 7a, c, 9b).

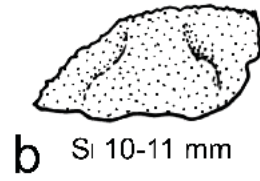
The pelvic girdle is only represented by the ilium and ischium (Text-fig. 12h–l). The ilium is well ossified, with a wide mid-shaft. The dorsal process is short, only slightly inclined backwards on the ventral margin, and is dorsally widely expanded. Its shape differs from that of the other *Branchiosaurus*-species.

The ilium has a more elongated dorsal process which is more inclined backwards in *B. salamandroides* (Text-fig. 12o–t). In *B. commentryensis*, it has a slender dorsal process which is more inclined backwards (Text-fig. 12m, n). The inclination posteriorly alone is somewhat stronger in the Carboniferous species *B. salamandroides* and *B. commentryensis*. The mid-shaft of the ilium from *B. salamandroides* can also vary with an individual (Text-fig. 12p; compare the possible variability in Discussion). The ischium is elongated and narrow (Text-fig. 7d). It is shared with *B. salamandroides* and in contrast to *B. commentryensis* with a short and relatively wide shape.

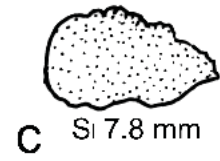
The scalation is well preserved in the largest specimen ($S_1 = 10\text{--}11$ mm; Text-fig. 2). In principle, this scalation consists of one type of scales organised in rows of the ventral, dorsal or lateral region. They are wide-oval or circular, well ossified and have up to 3 concentric rings or 5–6 straight, parallel marks. The radial and concentric pattern belong to different layers of one scale, as is known from well preserved scales of *Limnogyrinus elegans* (Werneburg 1994: 464,

Interclavicle

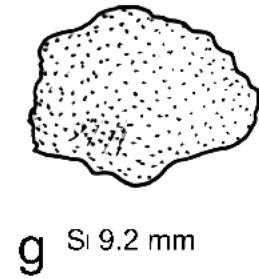
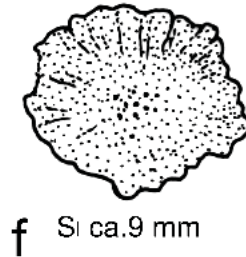
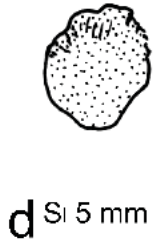
Branchiosaurus remesi



B. commentryensis

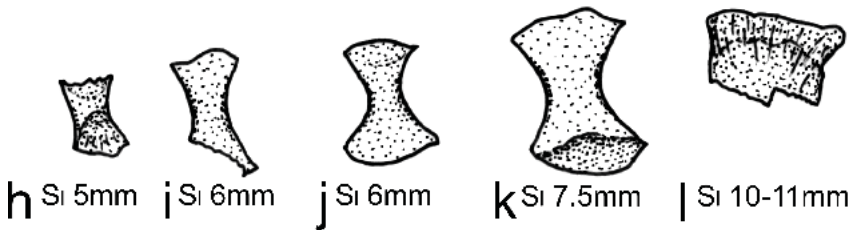


B. salamandroides

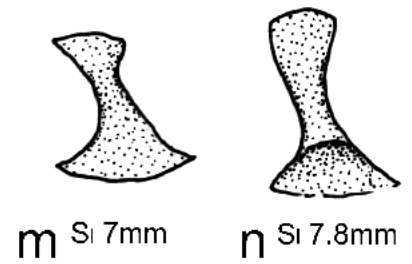


Ilium

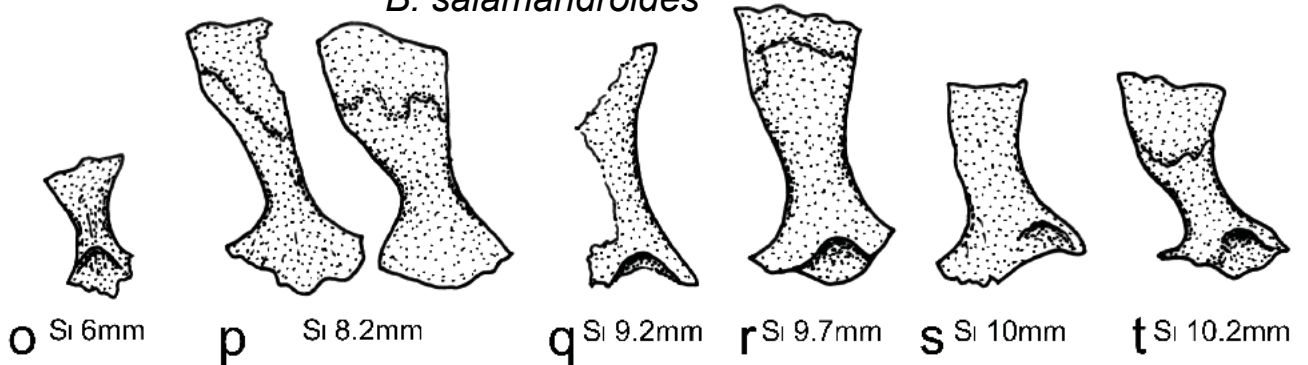
Branchiosaurus remesi



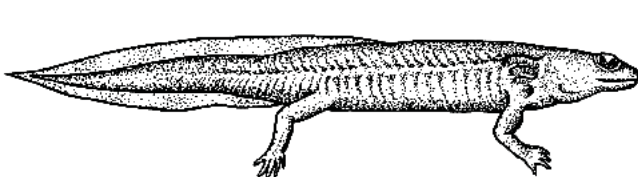
B. commentryensis



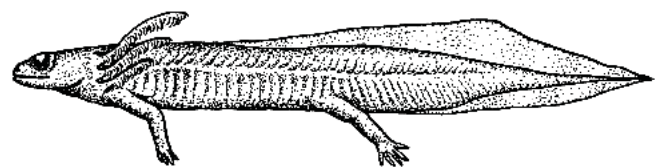
B. salamandroides



Text-fig. 12. Comparison of the interclavicle (a–g) and ilium (h–t) of the genus *Branchiosaurus*.



Stream-type



Pond-type

Text-fig. 13. Ecomorphotypes of Branchiosaurids.

fig. 8b). Therefore, the preservation with both radial and concentric elements is possible, but not together recorded in *B. remesi*. The ventral scales are more heavily ossified and thickened (but without distinct thicker posterior margins). The ventral scales are arranged in linear rows which are positioned in a V-shape on the ventral trunk side. Each scale overlaps the adjacent one in its row by half to two-thirds of its width, depending on the side of the abdomen. Moreover, successive rows of scales are arranged like roof tiles, with each anterior row partially covering the row behind it. The extent of overlap between the rows of scales depends on the current mechanical stress. In addition, each row of scales is covered like roof tiles by the front row to varying degrees, depending on the load. The extent of overlap between the rows of scales depends on the current mechanical stress. A peculiarity of one individual is that the scales are glued directly to the bones of the extremities (Text-figs 2, 3a; see Taphonomy and palaeoecology). The scales of the other two *Branchiosaurus* species are also broadly oval to circular in rows. *B. salamandroides* has up to 6 concentric rings and up to 9 radial striations (Werneburg 1987: fig. 8). In *B. commentryensis* the scale details are not well preserved.

Discussion

Affiliation. First, the reasons for the synonymy or validity of the genus and species will be discussed.

Genus. All 10 characters of the diagnosis of the genus *Branchiosaurus* (see above) are found in the material of ‘*Moraverpeton*’. Therefore, *Moraverpeton* AUGUSTA, 1947 is clearly a junior synonym of *Branchiosaurus* FRITSCH, 1876. This is the first time that a representative of the genus *Branchiosaurus* has been discovered in the Permian.

Species. First of all, the differences between *B. remesi* and the other two species of the genus *Branchiosaurus* must be pointed out. *B. commentryensis* differs from *B. remesi* in having the following characters:

- (1) Skull wide and short, it is 1.32 times wider than long.
- (2) Wide preorbital skull with shorter nasal + short and wide vomer.
- (3) Short-oval orbit (max. orbital length-to-width ratio: 1.16).
- (4) Very wide interorbital region ($IO_w/S_l = 0.32\text{--}0.38$)
- (5) Short squamosal.
- (6) Supratemporal elongated, clearly longer than wide.
- (7) Posteromedial sclerotic elements short and wide.
- (8) Basal plate of parasphenoid with carotid foramina and foramina for nervus palatinus VII.
- (9) Hyobranchial skeleton of *kontheri*-type.
- (10) Dorsal process of ilium more inclined posteriorly, possibly wider shaft of dorsal process.
- (11) Ischium short and relatively wide.

B. salamandroides differs from *B. remesi* in having the following characters:

- (1) Maxilla with about 35–36 teeth.
- (2) Premaxilla with 14–15 teeth.
- (3) Posteromedial sclerotic elements short and wide.
- (4) Basal plate of parasphenoid with carotid foramina and foramina for nervus palatinus VII.
- (5) Scales with 6 concentric rings and up to 9 radial striations.

(6) Dorsal process of ilium more inclined posteriorly, which is possibly longer.

B. remesi from Moravia is most similar to *B. salamandroides* from Bohemia, but there are 6 practicable differences. Therefore, *Branchiosaurus remesi* (AUGUSTA, 1947) is clearly a valid species of the genus *Branchiosaurus*.

Variability and Relationships. Some characters vary and several implement interesting relationships to other taxa and lead to new ideas. The pterygoid from the palate of one individual differs in having a more pronounced transverse process on its palatine branch and a much more elongated basipterygoid branch (Text-figs 6b, 10c) than in other specimens from the same species. The first character is a plesiomorphy, but the elongated basipterygoid branch is more interesting. Indeed, the last variant of *B. remesi* is shared with *Piasimotriton kochovi* from much younger beds (Sakmarian) of the Boskovice Basin (Werneburg et al. 2023), *Milnererpeton huberi* from the Late Pennsylvanian of New Mexico (Werneburg et al. 2013, 2021), the late adult *Apateon caducus* from the Asselian of Germany (Werneburg 2020) as well as a few lissamphibians (Werneburg et al. 2023).

Another example is the shape of the ilium from the pelvic girdle. It differs from that of the other *Branchiosaurus*-species (see description above). The ilium in *B. salamandroides* has a more elongated dorsal process which is more inclined backwards (Text-fig. 12o–t). *B. commentryensis* has a slender dorsal process which is more inclined backwards (Text-fig. 12m, n). However, we only know of about fifty specimens from the genus *Branchiosaurus* and the variability may also have been higher in that genus, as recorded from *Apateon dracyiensis* with about 3,500 specimens (Werneburg 2021: fig. 32a–s). Amongst this material was found an additional Morphotype S with a different shape of the ilium and femur. The Morphotype S is rare, representing only about 1 % of all specimens of *A. dracyiensis* of the taphocoenose from the Cabarz Quarry (Goldlauter Fm.) in the Thuringian Forest. It bears a stronger, shorter and more robust ilium as well as stronger limb bones though presenting a skull architecture similar to all other specimens of *A. dracyiensis* (Werneburg 2021). Finally, all proportions of the ilium recovered from the *Branchiosaurus*-species (Text-fig. 12h–t) fall in the variability range of *A. dracyiensis*.

On the other side, not all these morphotypes of the ilium fall in the variability range of *A. pedestris* or *A. flagrifer*, which are also recorded with thousands of specimens (Boy 1972, Schoch 1992, Werneburg 1986). *A. dracyiensis* shares some characters with *Branchiosaurus*, for examples the contact of pre- and postfrontal or the shape of the interclavicle and ilium. Many other characteristics are different, so that *A. dracyiensis* does not belong to the genus *Branchiosaurus*. However, this species is also not a typical member of the genus *Apateon* like *A. pedestris* or *A. flagrifer*. *Piasimotriton* also shows references to *Branchiosaurus*, e.g., the square supratemporal, the shape of the ilium and pterygoid. This indicates a relationship between the two genera.

Taphonomy and palaeoecology

All amphibian remains from the type locality “Za pilou dolu Antonín” (dump behind the saw-mill of the Antonín-Mine) near

Zbýšov are preserved in pale gray, patchy ochre weathering mudstones of the Zbýšov Horizon. The mudstone is in 2 mm to 5 mm scale indistinctly bedded by grain size changes from silty to clayish. The aquatic fauna consists mainly of juvenile bivalves of 1.5 mm to 3 mm size; valves of 10 mm length are somewhat rare. They are very common and mostly articulated on certain bedding planes, but butterfly preservation is not rare. Indeterminable conchostracans are rare (taphonomic effect?), as well as small actinopterygian fishes of estimated 3 cm to 4 cm length, and *Acanthodes* spines. Spiral coiled heteropolar coprolites of up to 6 cm length point to the presence of freshwater sharks (Hunt and Lucas 2012).

Besides mm-sized plant detritus on bedding planes, rare fragments of the algae *Perissothallus* as well as a 3 cm-wide and minimally 13 cm-long bundle of *Perissothallus* cf. *dekovensis* PŠENIČKA et KRINGS, (Pšenička and Krings 2016) were observed. In places 2 mm- to 4 mm-wide plant roots occur on slabs with bivalves. On a sandier slab from the mine dump an about 5 cm long indeterminable tetrapod footprint was found. From the same locality the blattoid insects *Phyloblatta flabellata* (GERMAR, 1842) and *Opsiomylacris* cf. *procerus* HAUPT, 1952 were described by Schneider (1980, 1984).

The branchiosaurids found here also reveal some palaeo-ecological details. The external gills of *Branchiosaurus remesi* are short (Text-figs 2, 5a, b, f; Werneburg 2001). Therefore, the population from the Zbýšov Horizon belongs to the stream type in analogy to recent salamander larvae (Text-fig. 13; Werneburg 2002). Unfortunately, the caudal fin as second character of this type is not preserved. This ecomorphotype mostly settled in small lakes, ponds, pools of flood plains with a high content of oxygen in a widespread alluvial landscape (Werneburg 2009).

One intestine content probably includes carbonized wood substance, partly with imprint of linear crossed wood structures, both between the ventral scale rows and the vertebral column (Text-figs 2, 3). This could be wood that was accidentally washed in. However, such a small piece of wood lies to the right of the trunk and is preserved as an imprint only and not as charcoal. It may be that the charcoal-like substance in the area of the intestines is heavily digested plant remains, which may have spelled its end.

Even if the samples came from a mine dump and not from a section, lithofacies, bedding types, and fossil content allow the palaeoecological characterisation of the depositional environment. Augusta (1947) has described it as deposits of a small lake with swampy and marshy shores, vegetated by *Calamites* and *Sphenophyllum*. Based on our finds from 1991 and 2005, the depositional environment of the beds with the branchiosaurids could be interpreted as follows: common bivalves, especially juvenile ones, and the occurrence of *Perissothallus* and roots of plants point to littoral deposits, specifically to the eulittoral and sublittoral zones with submersed plants and algae. The tetrapod track may come from the supralittoral. Predatory actinopterygians and discosauriscids obviously did not live in this small lake. Only xenacanthids seem to have visited the lake occasionally as concluded from the rare occurrence of teeth. The predation pressure was consequently low. The plankton feeder *Acanthodes* and the rare small actinopterygians may have competed for food with the branchiosaurids, but were comparatively rare. In addition, they were not found together with branchiosaurids on the

same bedding planes and therefore could not have lived in the lake together with the latter at the same time. In conclusion, this lake was at times amphibian dominated. Since only the stream-type of *B. remesi* was found, it can be assumed that the oxygen content in the water was high, possibly due to inflow from a river. The population of *B. commentryensis* from the lake Commentry belongs to the stream-type with short external gills and low caudal fin (Werneburg 2019). Traces of external gills or caudal fins from the specimens of *B. salamandroides* of the lake Nýřany are not recorded (Werneburg 2012).

In contrast, the Moravský Krumlov lake was fish-dominated. Besides only one *Branchiosaurus* skeleton, numerous remains of the actinopterygian *Neslovicella* and common teeth and spines of the freshwater shark *Bohemiacanthus* were sampled. Even if *Neslovicella* was only 6 cm to 7 cm long, it could have competed with *Branchiosaurus* for food if it occurred frequently. Freshwater sharks seem to have been more common in Moravský Krumlov than in Zbýšov and may have caused predation pressure.

Alternations between fish-dominated and amphibian-dominated lake stages are known from numerous early Permian basins in Europe (e.g., Boy 1972, Werneburg 2002, Werneburg et al. 2007, Schneider et al. 2024). These changes are caused by the interference of various aut- and synecological factors, such as oxygen levels, which favour the exclusively gill-breathing fishes or the gill- and lung-breathing amphibians differently, as well as food competition and predator pressure. Lake Kochov in the Letovice Formation of the Boskovice Basin is an example of this, which was analysed in detail by Werneburg et al. (2023). It is assumed that in lake Kochov, the large actinopterygians *Paramblypterus* and *Bourbonnella* competed with discosauriscid amphibians for the same prey, the aquatic arthropods, such as ostracods and conchostracans. Additionally, the dominance pattern in this lake is most likely caused by changing oxygen content; well oxygenated – fish lake, poorly oxygenated – amphibian lake. Interestingly, in the section of this lake, branchiosaurids appear in only a 10 cm thick fish- and discosauriscid-free bed. Therefore, the rare occurrence of branchiosaurids in the Boskovice Basin in general seems to be mainly caused by the predominance of discosauriscids, which occupied the ecological niche which is in the most other early Permian basins of Europe occupied by branchiosaurids.

Conclusions

The branchiosaurid *Branchiosaurus remesi* (AUGUSTA, 1947) found in the Zbýšov Horizon of Padochov Formation (earliest Asselian, early Permian) from Zbýšov and Moravský Krumlov in the Boskovice Basin (Moravia, the Czech Republic) is revised and allowed the following conclusions regarding its taxonomy, relationships and palaeoecology.

(1) The original amphibian material of Zbýšov from Augusta (1947) is very probably lost. Augusta (1947) described ‘*Moraverpeton remesi*’ and assigned it to the family Branchiosauridae. But Augusta (1947) described an “interclavicle with a long and strike processus at the back” which is a typical feature of *Discosauriscus*. However, this posterior process is not recognizable on his photos and it is highly questionable. All other features of *Moraverpeton* described

by Augusta (1947) clearly fit that of branchiosaurids. He mentioned ossified gill rakers and 20–22 presacral vertebrae which were clear-cut characteristics of branchiosaurids and not known from seymouriamorphs (no gill rakers and 23–24 presacrals, see Klembara and Bartík 2000). Augusta (1947) reported as second amphibian *Branchiosaurus* sp. in bad preservation without characteristics. Overall, the branchiosaurid nature of '*Moraverpeton*' *remesi* AUGUSTA, 1947 is highly probable.

(2) New branchiosaurid material from the Zbýšov Horizon of Zbýšov and Moravský Krumlov is hereby figured and described and we assume that it is consistent with the described amphibian material from Augusta (1947). This material forms the basis for the revision of '*Moraverpeton*' *remesi*.

(3) '*Moraverpeton*' *remesi* AUGUSTA, 1947 clearly belongs to the family Branchiosauridae FRITSCH, 1879, and to the genus *Branchiosaurus* FRITSCH, 1876. The diagnosis of *Branchiosaurus* is adapted to all three members of this genus. All 10 characteristics are detectable in *Branchiosaurus remesi* (AUGUSTA, 1947). *B. remesi* has e.g., a contact of prefrontal-postfrontal, an anteriorly extended jugal even at an early stage, branchial denticles with elongated single needle or paired needles – mostly attached to a rounded base, ventral osteoderms well ossified and thickened in a V-shape.

(4) *B. remesi* is a valid species in the genus *Branchiosaurus*. It differs from *B. commentryensis* in 11 features and from the closer related *B. salamandroides* in 6 characters.

(5) One well preserved skeleton has been established as the neotype of *B. remesi* (NHMS-WP751a, b). This species is defined by a unique character combination of 11 features. *B. remesi* has e.g., a narrow preorbital skull, squarish supratemporal, elongated and narrow posteromedial sclerotic elements and a hyobranchial skeleton of the *flagrifer*-type.

(6) The aquatic biota of the Zbýšov lake consists mainly of juvenile bivalves, and rarely conchostracans, small actinopterygian fishes, *Acanthodes*, freshwater sharks and algae. This lake was at times amphibian dominated. The population of *Branchiosaurus remesi* from this lake belongs to the stream type because of their short external gills. Therefore, it can be assumed that the oxygen content in the lake was high, possibly due to inflow from a river. A tetrapod footprint and several insects document the neighbourhood of terrestrial animals. The aquatic fauna of the Moravský Krumlov lake was fish-dominated by actinopterygians and xenacanthids, consequently branchiosaurids are very rare there because of predator pressure.

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